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Acleistochelys, a New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Paleocene of Mali

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ABSTRACT

The Paleocene Teberemt Formation south of the Adrar des Iforas Mountains, between Saguirilidad and In Fargas, Mali, yielded a nearly complete skull of a new genus and species of side-necked turtle, *Acleistochelys maliensis*. *Acleistochelys* is a member of the family Bothremydidae Baur, 1891, because: (1) the fossa precolumellaris is absent, (2) the foramen stapedio-temporale faces anteriorly, (3) the eustachian tube is separated from the stapes by bone, and (4) an exoccipital-quadrate contact is present. Within the Bothremydidae, *Acleistochelys* belongs to the tribe Taphrosphyini because: (1) the maxilla-quadratojugal contact is absent, (2) the palate is dorsally arched, (3) there is only a small contribution of the palatine to the triturating surfaces, and (4) the septum orbitotemporale is at least partially open. *Acleistochelys* is most closely related to *Azabbaremys* because both share a narrow vomer lacking a posterior attachment to the palatines.

The specimen was found in a marine limestone associated with crocodiles, echinoids, and mollusks.

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INTRODUCTION

The Bothremydidae is an extinct group of side-necked turtles recently reviewed and expanded in content by Gaffney et al. (2006). The purpose of the present paper is to name and describe a new bothremydid, based on CNRST SUNY 199 from the Paleocene of Mali (Tapanila et al., 2004). The skull description follows the outline in Gaffney et al. (2006: appendix 1) for ease of comparison with other bothremydids. Based on the phylogenetic analysis of Gaffney et al. (2006), *Acleistochelys maliensis* is a member of the tribe Taphrosphyini as characterized in Gaffney et al. (2006). Figures, descriptions, and references to all of the bothremydid taxa referred to in this paper can be found in Gaffney et al. (2006). The taxonomy also follows that reference. The skull here named *Acleistochelys maliensis* is included in the data set of Gaffney et al. (2006: appendix 3) and is shown in cladograms in figs. 288–314 as CNRST SUNY 199. The reader should see this work for further discussion of this phylogenetic analysis.

Institutional Abbreviations

AMNH	American Museum of Natural History, New York
CNRST SUNY	Centre National de la Recherche Scientifique et Technologique, Bamako, Mali–Stony Brook University, New York
FMNH	Field Museum of Natural History, Chicago

Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid
ex	exoccipital
fpcci	foramen posterius canalis carotici interni
fr	frontal
ju	jugal
mx	maxilla
na	nasal
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal
vo	vomer

GEOLOGY

Geological Setting

During the latest Cretaceous (Campanian–Maastrichtian) through middle Eocene, the Trans-Saharan Seaway inundated portions of central West Africa (Petters, 1979). In northern Mali, three transgressive–regressive cycles are recorded by a relatively thin (<100 m) sequence of sedimentary strata dominated by sandstones, shales, limestones, and phosphates (e.g., Radier, 1959; Bellion et al., 1989; Moody and Sutcliffe, 1993; Tapanila et al., 2004). These units were deposited in terrestrial, marginal marine, and open marine settings within and along the margins of the Trans-Saharan Seaway, and they preserve a rich vertebrate and invertebrate fossil record.

The Late Cretaceous–Paleogene Malian outcrops that are the focus of this study (fig. 1) are located in a narrow, half-graben structure, known as the Gao Trench or "Detroit Soudanais." Paleontologic investigations of invertebrate faunas demonstrate that the Trans-Saharan Seaway may have provided at times a dispersal route via the Gao Trench for marine fauna between the Tethys Sea and South Atlantic Ocean (Kogbe, 1981; Moody and Sutcliffe, 1993). Today this vast, desolate region is characterized by expansive low-relief plateaus that are capped by resistant limestone beds. Small shifting dune fields and vast stretches of desert pavement cover this region and obscure regional stratigraphic correlations.

Sedimentology of Mali 17

Description

The turtle specimen described herein was recovered from locality Mali 17, located south of the Adrar des Iforas Mountains, between

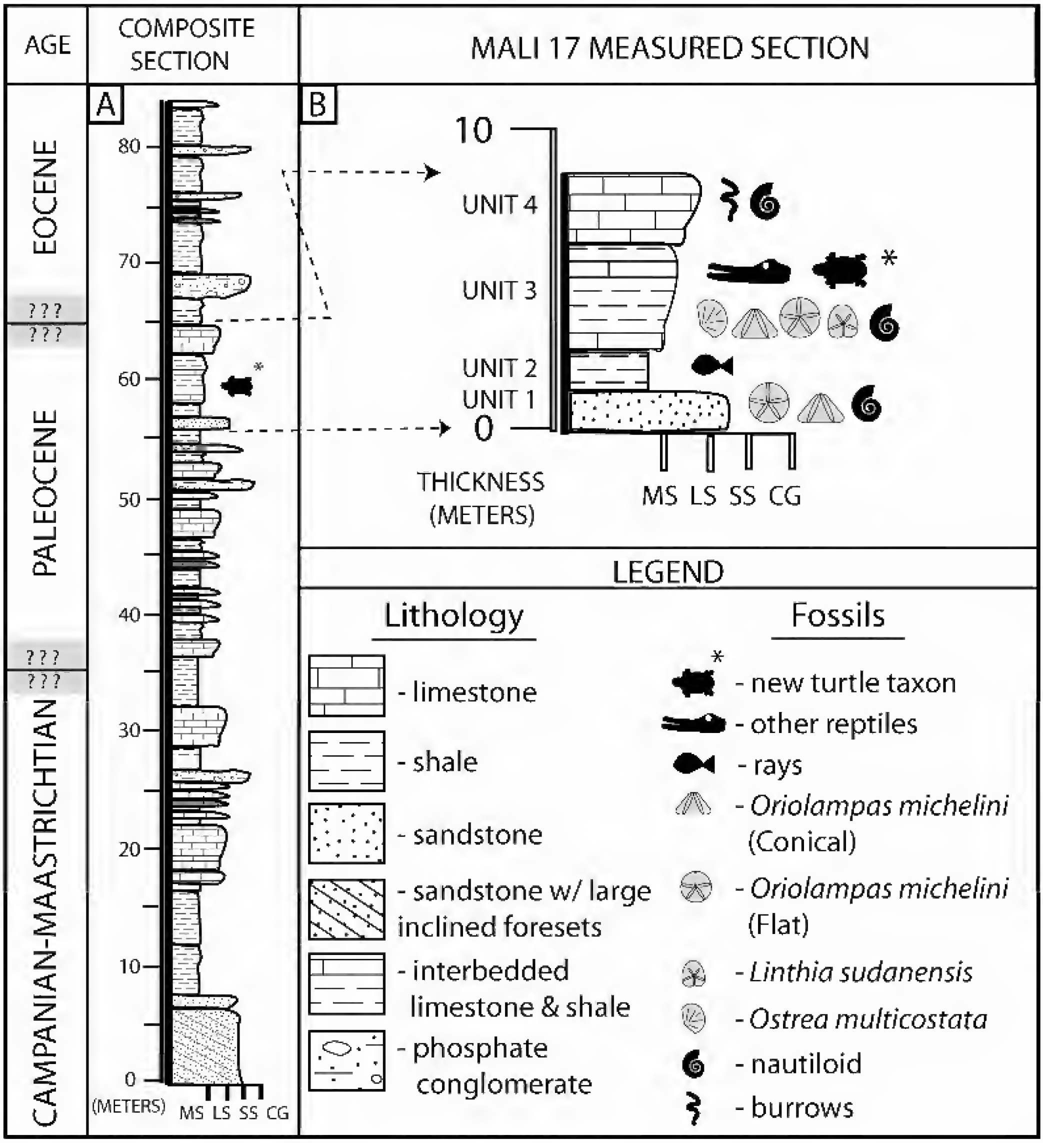

Fig. 1. Stratigraphic section of locality Mali 17, showing position of type specimen of *Acleistochelys maliensis* n.gen., n.sp.

Saguirilidad and In Fargas. Mali 17 is situated within a 6–10 m thick sequence of richly fossiliferous phosphatic sandstones, shales, and limestones. The sedimentology at Mali 17 is characterized by a basal 1 m thick white to pale yellow phosphatic sandstone (unit 1) with nodular chert concretions that grades upward into a thin (0.5 m), dark gray sandy shale (unit 2) containing ray tooth plates and abundant bioturbation (fig. 1b). A 3 m thick chalky, micritic limestone with thin shale partings (unit 3) overlies this unit and preserves multiple articulated and associated turtle remains, including the specimen described in this report. Other well-preserved vertebrate and invertebrate fossils were also recovered from this laterally extensive bed, including the remains of crocodiles, encrusting oysters (*Ostrea multicostata*), nautiloids (*Deltoidonautilus* sp.), gastropods (*Gistortia*

sp.), and echinoids (e.g., *Linthia sudanensis, Oriolampas michelini*). The entire succession is capped by a distinctive 2 m thick, cliff-forming, blocky, recrystallized limestone bed (unit 4). This unit preserves rare, moldic nautiloids and abundant trace fossils.

Interpretation

Mali 17 represents an upward fining, retrogradational marine sequence. Increasing water depth is interpreted based on reduction of siliciclastics and increasing purity of carbonates upward through the sequence. The fauna recovered from Mali 17 are consistent with relatively low-energy, normal marine conditions.

Strata of Mali 17 likely belong to the middle to upper portion of the Teberemt Formation of Moody and Sutcliffe (1991, 1993), which they interpreted as Paleocene. Paleogene echinoderms, such as *Oriolampas michelini* and *Linthia sudanensis*, recovered from the turtle-bearing unit 3 preclude a Cretaceous age assignment, while putative Eocene (Ypresian) vertebrates documented from stratigraphically higher phosphate conglomerates (fig. 1A; ~68 m level) at nearby Tamaguilelt (Pascal and Traore, 1989; Patterson and Longbottom, 1989; Moody and Sutcliffe, 1993; O'Leary et al., 2006) provide an upper age limit. Moody and Sutcliffe (1993) also correlated the Teberemt Formation with a similar stratigraphic sequence on the west side of the Tilemsi valley, near Tichet, which Bellion et al. (1989) dated as late Paleocene using benthic foraminifera and ostracodes. Based on faunal analysis and detailed outcrop correlation with strata exposed below and above Mali 17, we tentatively agree with the Paleocene age assignment of Moody and Sutcliffe (1991, 1993) for these deposits, although an early Eocene age cannot necessarily be precluded.

SYSTEMATICS

ORDER TESTUDINES LINNEAUS 1758 OR BATSCH 1788

INFRAORDER PLEURODIRA COPE, 1864

FAMILY BOTHREMYDIDAE BAUR, 1891

TRIBE TAPHROSPHYINI GAFFNEY, TONG, AND MEYLAN, 2006

SUBTRIBE TAPHROSPHYINA GAFFNEY, TONG, AND MEYLAN, 2006

Acleistochelys, new genus

TYPE SPECIES: *Acleistochelys maliensis*, new species.

DISTRIBUTION: Paleocene of Mali.

ETYMOLOGY: *Aklystos*, Greek for "sheltered", or "hollowed", in allusion to the small, paired pits on the triturating surface; *chelys*, Greek for "turtle".

DIAGNOSIS: A bothremydid pleurodire with these unique characters among the tribe Taphrosphyini: small pit formed by jugal, maxilla, and palatine on triturating surface; jugal exposed on triturating surface; accessory ridge present on anterior triturating surface; wide palatine-basisphenoid contact separating pterygoids on midline; supraoccipital-quadrate contact present; basioccipital narrowly enters condylus occipitalis; palatine-jugal contact in small septum orbitotemporale. Other distinguishing characters are: skull relatively long and narrow; fossa pterygoideus deep and narrow as in *Nigeremys* but in contrast to *Taphrosphys*; foramen posterius canalis carotici interni formed by pterygoid, basisphenoid, and quadrate in contrast to *Phosphatochelys*; small remnant of septum orbitotemporale present consisting of ventral parietal process as in *Phosphatochelys* but in contrast to *Taphrosphys*.

DISCUSSION: See table 1 for a comparison of genera in the tribe Taphrosphyini.

Acleistochelys maliensis, new species

TYPE SPECIMEN: CNRST SUNY 199 (figs. 2–5), partial skull including fragments of the lower jaw, lacking some of the left temporal region, and both posterior parts of the skull roof. Skull measurements are in table 2. Associated shell fragments include the anterior margin of the nuchal (fig. 6), neurals one and four (fig. 7), and peripheral two (fig. 7). A partial cervical vertebra (figs. 8, 9) and some pelvic fragments are present.

TYPE LOCALITY: Mali 17, located south of the Adrar des Iforas Mountains, between Saguirilidad and In Fargas, Mali.

HORIZON: Middle to upper portion of the Teberemt Formation of Moody and Sutcliffe (1991, 1993).

DEPOSITIONAL ENVIRONMENT: Near shore marine.

DIAGNOSIS: As for genus.

ETYMOLOGY: Named for the country of discovery.

REFERRED MATERIAL: None.

PREVIOUS WORK: CNRST SUNY 199 is included in the phylogenetic analysis of Gaffney et al. (2006).

DESCRIPTION

PREFRONTAL

Preservation: Both prefrontals are present: the right one is nearly complete, the left is missing some of its lateral edge.

Contacts: The prefrontal in *Acleistochelys* has the same contacts as in *Azabbaremys*, *Nigeremys*, and *Arenila*: prefrontal on midline, maxilla anteroventrally, and frontal posteriorly. There is no palatine or parietal contact.

Structures: The dorsal plate of the prefrontal in *Acleistochelys* is similar to that in *Azabbaremys*, but not strongly convex dorsally as in *Azabbaremys*. The dorsal margin of the apertura narium externa in *Acleistochelys* is well posterior to the ventral margin in contrast to *Azabbaremys* in which the dorsal margin is almost directly above the ventral margin.

The size of the fossa nasalis and sulcus olfactorius are similar in both *Acleistochelys* and *Azabbaremys*. The ventral process of the prefrontal is narrow in *Acleistochelys*.

FRONTAL

Preservation: The right frontal in CNRST SUNY 199 is nearly complete; it is missing only its posterolateral corner. The left one is missing most of its lateral half.

Contacts: The frontal in *Acleistochelys* contacts the prefrontal anteriorly, the other frontal medially, the postorbital posterolaterally, and the parietal posteriorly, all as in *Azabbaremys*, *Nigeremys*, and *Arenila*, and in contrast to *Phosphatochelys* and *Rhothonemys*, which lack a postorbital contact.

Structures: The frontal in *Acleistochelys* enters the orbital margin, similar to that seen in *Azabbaremys* and *Nigeremys*.

PARIETAL

Preservation: Both parietals are present but damaged. The dorsal plate on the left side retains only its anteromedial portion. The right dorsal plate is more complete laterally, but it also lacks all of the temporal margin. The processus inferior parietalis, however, is nearly complete on both sides, the left one having some breakage ventrally.

Contacts of dorsal plate: The dorsal plate in CNRST SUNY 199 preserves the midline parietal contact and the medial part of the frontal contact anteriorly. The right parietal has the anterolateral contact with the postorbital preserved.

Structures of dorsal plate: The degree of temporal emargination in *Acleistochelys*, although not determinable exactly, was probably not as extensive as in *Nigeremys*, because the remaining broken margin is relatively thick and extends about as far as the natural margin in *Nigeremys* (and probably *Arenila*, although that skull also lacks most of the parietal dorsal plate).

The septum orbitotemporale (see Gaffney et al., 2006: fig. 78) in the tribe Taphrosphyini, may be reduced or absent (Gaffney et al., 2006: character 28). This is best seen in *Phosphatochelys* (Gaffney et al., 2006: fig. 202). However, the group that lacks the septum (that is, *Taphrosphys*, *Labrostochelys, Rhothonemys, Ummulisani*) also lacks the ventral parietal process seen in *Phosphatochelys* (Gaffney et al., 2006: fig. 202). This process is a remnant of the lateral wall of the septum orbitotemporale and reaches the palatine above the base of the processus trochlearis pterygoidei lateral to the sulcus palatinopterygoideus. This process also occurs in *Acleistochelys*, although there are differences from *Phosphatochelys*: In *Acleistochelys* it is thinner and longer, and contacts the palatine only, whereas in *Phosphatochelys* it is wider and shorter and contacts the palatine anteriorly and the pterygoid posteriorly. The entire ventral portion of the septum orbitotemporale remnant differs in *Acleistochelys*

TABLE 1
Genera of the Tribe Taphrosphyini

	Taphrosphys	*Labrostochelys*	*Azabbaremys*	*Phosphatochelys*	*Nigeremys*	*Arenila*	*Rhothonemys*	*Ummulisani*	*Acleistochelys*
Prefrontal extremely long and narrow	no	yes	no	no	no	no	no	no	no
Apertura narium externa at least partially divided	no	yes	no	no	no	no	yes	yes	no
Frontal in orbital margin	yes	yes	yes	no	yes	yes	yes	no	yes
Jugal	narrow	narrow	broad	broad	?	?	broad	?	broad
Squamosal with vertical flange	yes	yes	no	yes	?	?	yes	yes	no
Squamosal elongated posteriorly	no	yes	no	no	no	?	?	no	yes
Quadratojugal-jugal contact	present	present	present	absent	?	?	?	absent	?
Skull long and narrow	no	yes	no	no	no	no	no	no	yes
Skull short	no	no	yes	yes	no	no	no	yes	no
Premaxilla projects past labial ridge	no	yes	yes	no	yes	?	yes	yes	no
Basioccipital enters condylus occipitalis	no	no	no	no	?	no	?	no	yes
Apertura narium externa	small	small	small	large	small	?	large	large	small
Prefrontal horn	no	no	no	no	no	no	no	yes	no
PF-PAR contact	no	no	no	yes	no	no	no	yes	no
Jugal exposed on triturating surface	no	no	no	no	no	no	?	no	yes
Palatine-jugal contact in septum orbitotemporale	no	?	no	no	?	no	?	?	yes
Parietal forming at least part of septum orbitotemporale	no	?	no	yes	?	no	no	?	yes
Pit on triturating surface	?	no	no	no	no	no	no	no	yes
Accessory ridge on anterior part of triturating surface	no	no	no	no	no	no	?	no	yes
Wide palatine-basisphenoid contact	no	no	no	no	probably no	no	?	no	yes
SQ-QU contact	no	no	no	no	?	?	no	no	yes
Prefrontal extends to anterior edge of premaxilla	no	no	yes	no	no	?	no	no	no
Cheek emargination	yes & no	no	no	yes	no	no	?	no	no
Preorbital region very short	no	no	no	yes	no	no	no	no	no
Very large quadrate covering half of cheek	no	no	no	yes	?	?	?	yes	no
Foramen nervi trigemini trough	no	no	no	yes	?	no	?	yes	no
Antrum postoticum	small	small	absent	small	absent	?	small	absent	absent
Sulcus eustachii open more ventrally	yes	no	no	no	no	?	no	no	no
Interorbital width	narrow	very narrow	wide	wide	wide	wide	narrow	wide	wide

TABLE 1
(Continued)

	Taphrosphys	*Labrostochelys*	*Azabbaremys*	*Phosphatochelys*	*Nigeremys*	*Arenila*	*Rhothonemys*	*Ummulisani*	*Acleistochelys*
Parietal enters orbital margin	no	no	no	yes	no	no	yes	yes	no
Parietal forms postorbital wall and pocket	yes	?	no	yes	?	?	yes	yes	
Medial process of jugal	?	?	small	small	?	?	small	small	large
Maxilla deep	no	no	yes	yes	no	no	yes	yes	yes
Sulcus palatinopterygoideus	?	wide	wide	wide	narrow	narrow	?	narrow	wide
Ventrally opening channel at back of skull	yes	yes	no	no	no	?	?	no	no
Basisphenoid V-shaped	no	no	no	no	yes	yes	?	no	no
Basisphenoid pentagonal	yes	no	no	no	no	no	?	yes	no
Basisphenoid triangular and elongate	no	yes	no	no	no	no	?	no	yes
Vomer robust	?	no	no	?	yes	yes	?	?	no
Condylus mandibularis position in relation to condylus occipitalis	anterior	anterior	anterior	posterior	posterior	posterior	?	anterior	anterior
Fossa pterygoidei	absent	absent	absent	absent	deep & narrow	deep & narrow	?	absent	present
Septum orbitotemporale at least partially open	open	?	open	open	closed	closed	open	open	open
Prominent crenellations on triturating surface	no	no	yes	no	no	no	no	no	no
Triturating surface on maxilla thin curved trough	yes	yes	no	no	no	no	no	no	no
Labial ridge on maxilla	thin	thin	thick	thick	very thick	very thick	thick	thin	Thick
Maxilla-vomer contact	?	yes	no	Indet	yes	yes	?	?	no
Dorsally arched palate	no	no	yes	yes	yes	yes	?	no	yes
Cavum tympani	wider	wider	narrower	narrower	narrower	?	?	narrower	narrower
Sulcus eustachii with dorsal process	yes	yes	no	yes	?	?	yes	no	no
Sulcus eustachii with ventral process	yes	no	no	no	?	?	no	yes	no
Foramen posterius canalis carotici interni formed by	PT, BS, QU	PT, QU	PT, QU	PT, QU	?	BS, PT	?	QU & QU+PT	PT, BS, QU
Fenestra postotica	more vertical	more horizontal	more vertical	more vertical	more vertical	?	?	more horizontal	more vertical
Posteroventrally opening concavity on quadrate	yes	yes	no	no	no	?	?	no	no
Processus trochlearis pterygoidei very small	?	yes	no	no	no	no	?	no	no
Postorbital lacking medial process	?	no	yes	yes	no	no	yes	yes	yes

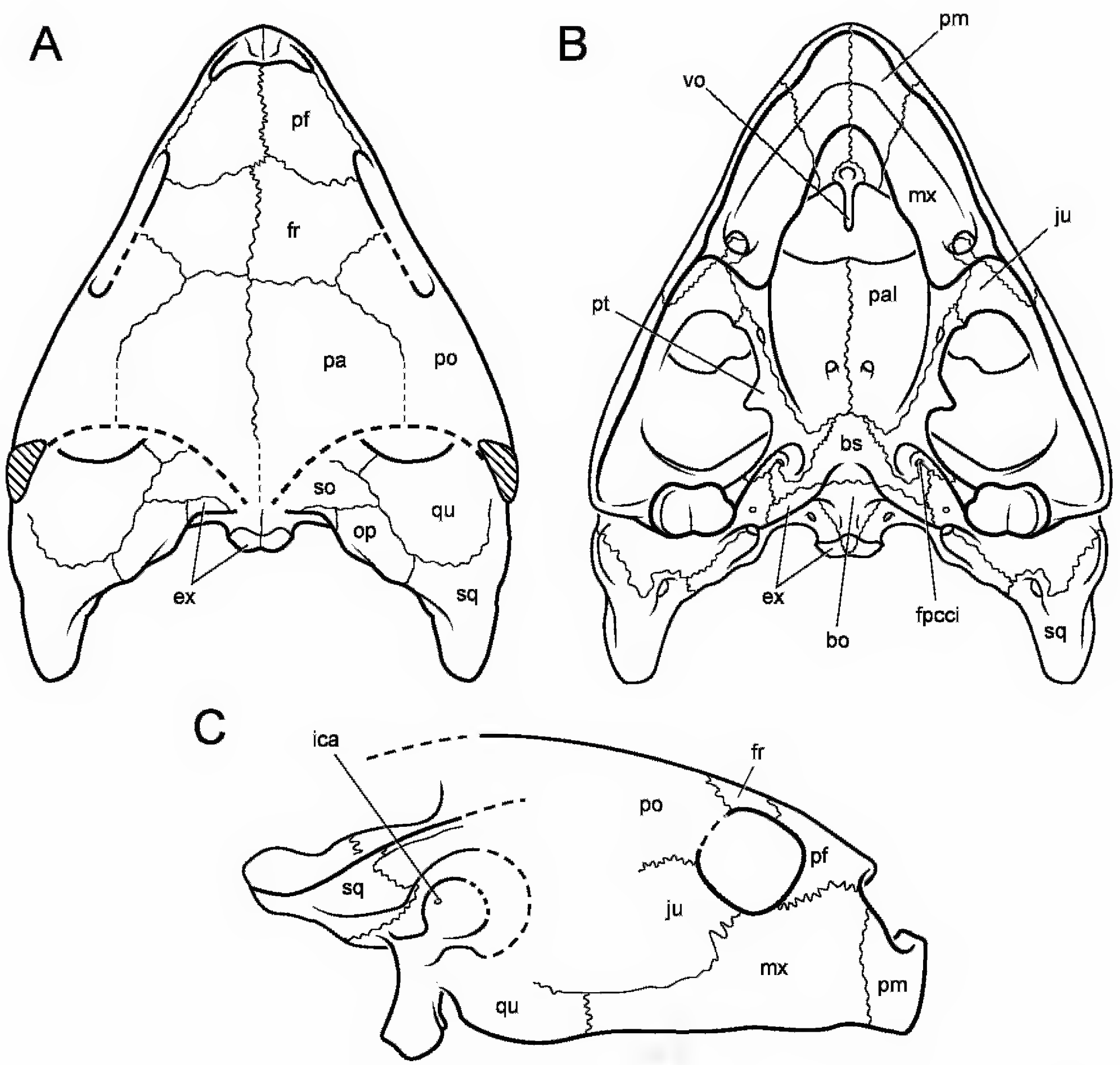

Fig. 2. *Acleistochelys maliensis* n.gen., n.sp. Partially restored skull based on CNRST SUNY 199. A, dorsal; B, ventral; C, right lateral.

and *Phosphatochelys* in the position of the jugal and palatine (see Jugal, Palatine). Whether this structure should be considered homologous in *Acleistochelys* and *Phosphatochelys* is a fascinating question.

Contacts of processus inferior parietalis: In *Acleistochelys* the vertical wall of the parietal contacts the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly. Although somewhat damaged, the processus inferior parietalis in *Acleistochelys* seems to be relatively thin, as in *Azabbaremys*, but still seems to contact the palatine, a condition that is unclear in *Azabbaremys*.

Structures of processus inferior parietalis: The foramen interorbitale is relatively large in *Acleistochelys*, as in *Azabbaremys* and *Phosphatochelys*, and the processus inferior parietalis is narrow, also as in

Fig. 3. *Acleistochelys maliensis* n.gen., n.sp. Partially restored ventral view of CNRST SUNY 199.

Azabbaremys. The foramen nervi trigemini, preserved on both sides, is formed by the usual bones: parietal anterodorsally, prootic posterodorsally, and pterygoid ventrally.

Jugal

Preservation: Neither jugal is complete, both are missing their posterodorsal margins. The left jugal preserves the ventral margin, and the right preserves the anterodorsal margin. The medial process on both sides is present.

Contacts of lateral plate: The jugal in *Acleistochelys* has a long anteroventral contact with the maxilla as in *Azabbaremys* and at least an anterodorsal contact with the postorbital, but the length of the bone is indeterminate. The jugal contacts the quadrate posteroventrally in a suture that is more

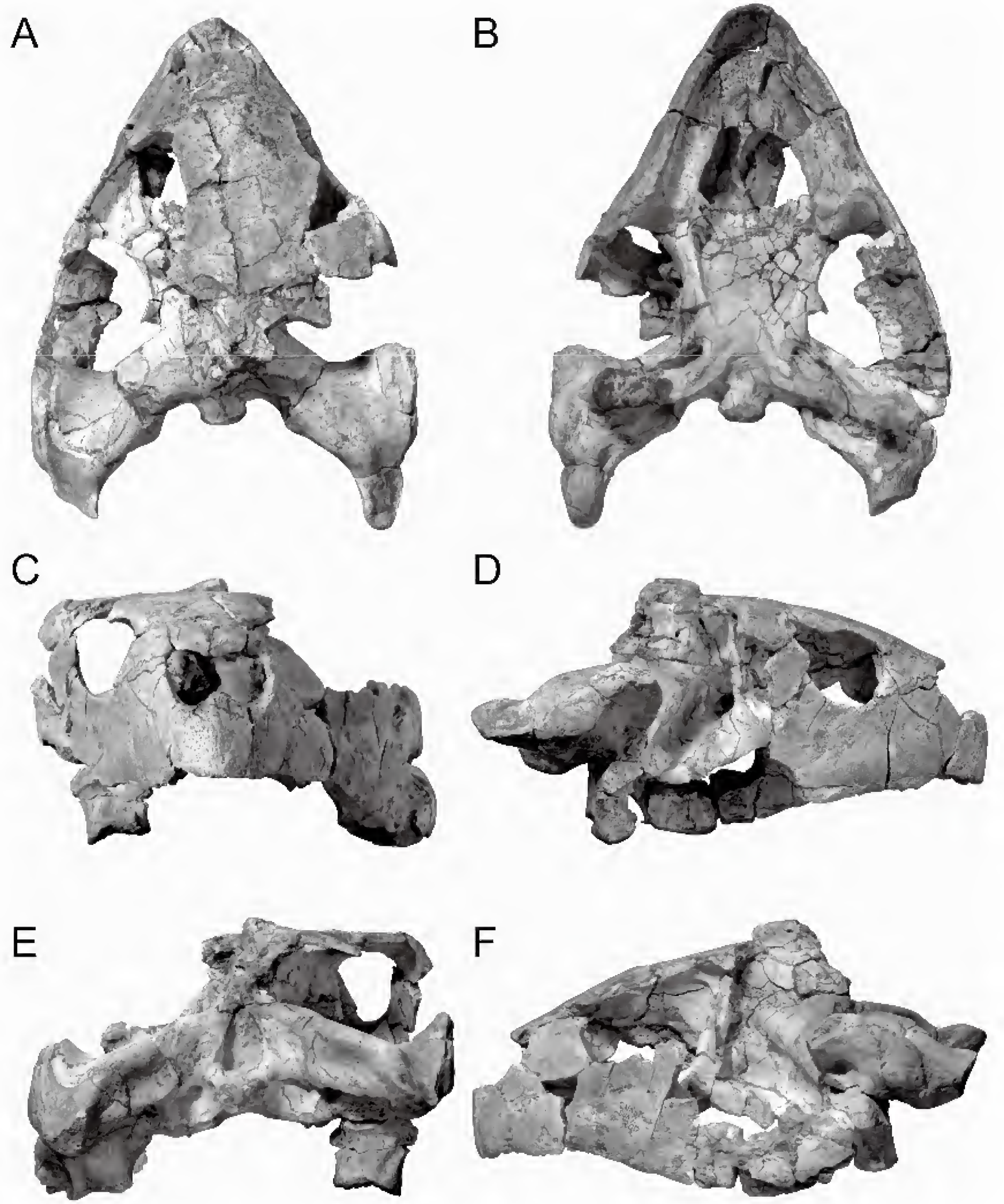

Fig. 4. *Acleistochelys maliensis* n.gen., n.sp. Photographs of CNRST SUNY 199. A. dorsal; B, ventral; C, anterior; D, right lateral; E, posterior; F, left lateral.

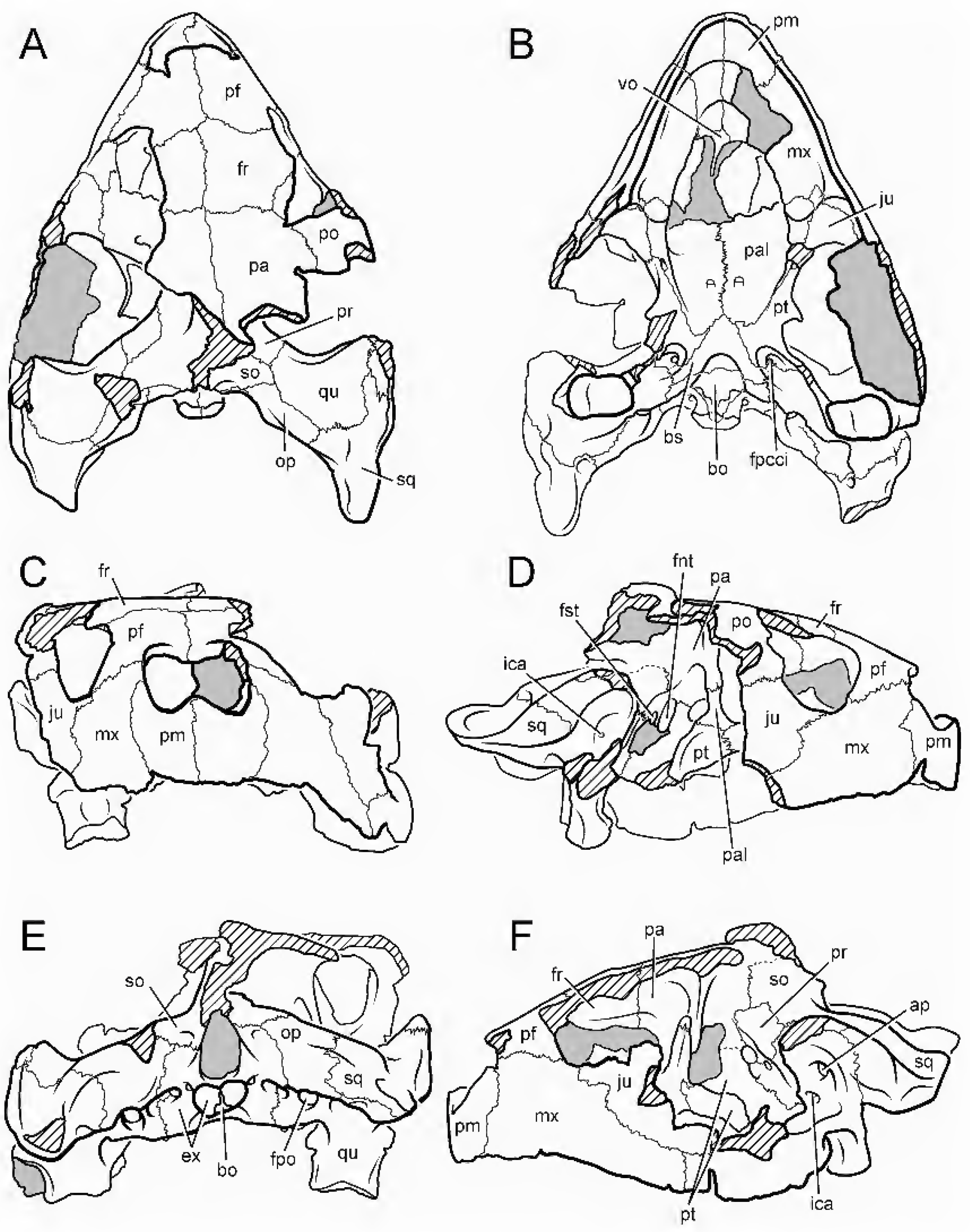

Fig. 5. *Acleistochelys maliensis* n.gen., n.sp. Line drawings of CNRST SUNY 199. A. dorsal; B, ventral; C, anterior; D, right lateral; E, posterior; F, left lateral.

horizontal than in *Azabbaremys*, showing that at least some of the jugal in *Acleistochelys* lies above the quadrate as in *Taphrosphys*, in contrast to abutting against it, as in *Azabbaremys*. Likely contacts with the quadratojugal are indeterminate due to the absence of that bone and that part of the jugal margin.

Structures of lateral plate: The jugal in *Acleistochelys* is relatively large and, to the extent preserved, similar to that in *Azabbaremys* in position and shape. The jugal forms the posteroventral margin of the orbit and is prevented from reaching the cheek margin by a quadrate-maxilla contact of the type seen in *Taphrosphys*, *Labrostochelys*, and *Azabbaremys*.

Contacts of medial process: The medial process of the jugal in *Acleistochelys* contacts the maxilla anteriorly, the pterygoid posteriorly, and the palatine medially, as in *Azabbaremys* and other Taphrosphyini. The jugal also contacts the palatine in the remnant of the septum orbitotemporale, lateral to the sulcus palatinopterygoideus. This is in contrast to the condition in *Azabbaremys*, which lacks that palatine contact and partial wall of the septum orbitotemporale. *Phosphatochelys*, however, does have a condition similar to that in *Acleistochelys*.

Structures of medial process: The medial process of the jugal is widely exposed in the orbital floor, more so than in *Azabbaremys* (Gaffney et al., 2006: fig. 280). The jugal forms a dorsally opening concavity in the floor of the fossa orbitalis, as in *Azabbaremys* but in contrast to AMNH 30521 in which the pocket is formed by the maxilla (Gaffney et al., 2006: fig. 211).

On the ventral surface the jugal in *Acleistochelys* is unique among Taphrosphyini in being exposed on the triturating surface, although the extent is much less than in other bothremydids (Gaffney et al, 2006: fig. 11). However, in *Azabbaremys* the jugal extends onto the margin of the triturating surface (Gaffney et al., 2006: fig. 215B) in a condition that isn't very far from that in *Acleistochelys*. As in the group consisting of *Bothremys* and its close relatives, the exposure of the jugal in *Acleistochelys* is apparently correlated with the development of a small pit, formed by the jugal, maxilla, and palatine. The jugal forms the tip and posterior wall with the maxilla anteriorly and laterally and the palatine medially. The triturating surface in *Acleistochelys* is narrow, as in other members of the Taphrosphyini, and in contrast to the wide surface of the Bothremydini, which

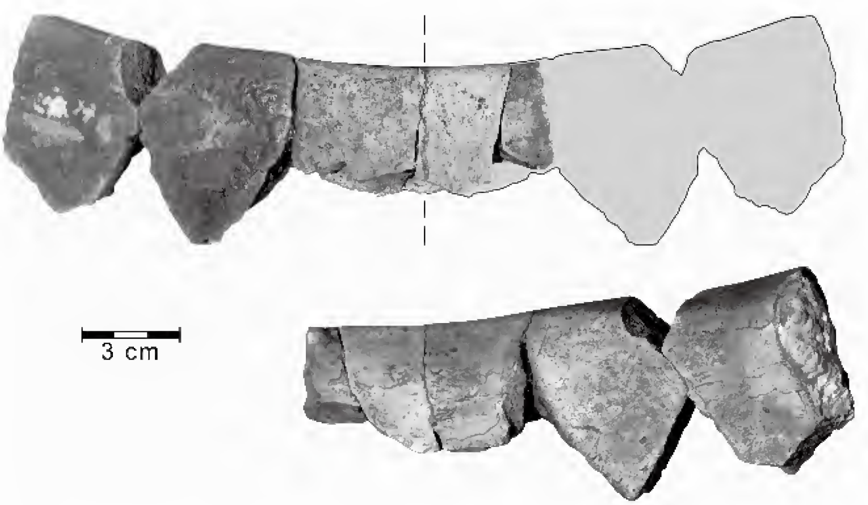

Fig. 6. *Acleistochelys maliensis* n.gen., n.sp. CNRST SUNY 199. Anterior margin of nuchal bone, dashed line indicates midline, sulcus separates the first pair of marginal scales. Upper, dorsal view, right half restored; lower, ventral view.

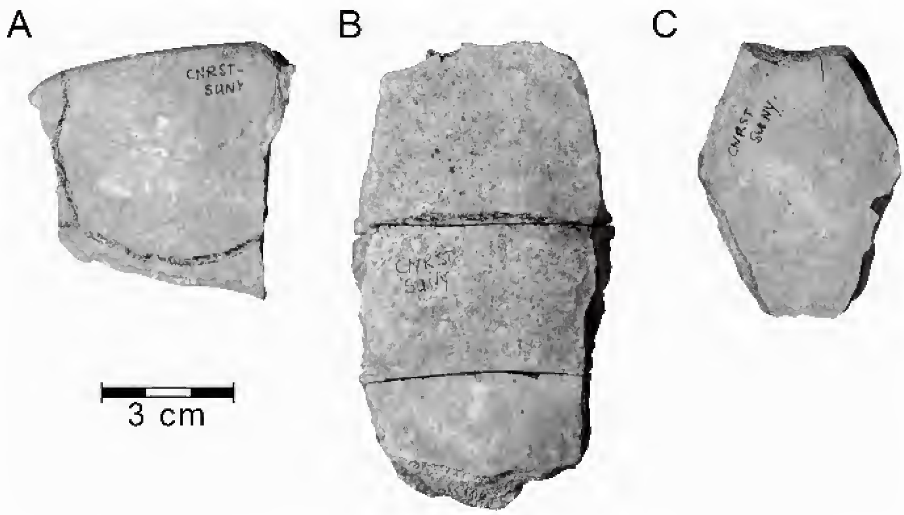

Fig. 7. *Acleistochelys maliensis* n.gen., n.sp. CNRST SUNY 199. Dorsal views of: A, posterolateral part of ?peripheral two; B, neural one; C, neural four.

accommodates the larger pit in that group. The pit in *Acleistochelys* is smaller and shallower, with poorly defined anterior and lateral margins in comparison to the ones in the Bothremydini. Nonetheless, it is a structure completely absent in any living turtle, but that arose independently within the Bothremydidae and an undescribed Moroccan cryptodire (Gaffney et al., 2006). Its function, other than cracking the odd walnut, remains enigmatic.

Quadratojugal

Preservation: Small fragments of each quadratojugal are suspended from each quadrate. The right one is more complete, but has broken anterior and dorsal margins.

Contacts: The quadratojugal fragment contacts the quadrate ventrally and the squamosal posteriorly, preventing quadrate exposure in the temporal margin. Although it may be slight, all bothremydids with the area preserved have a quadratojugal-squamosal contact. As in other members of the Taphrosphyini, there is no quadratojugal contact.

Structures: Although it is not preserved, the quadratojugal presumably reached the temporal margin.

Squamosal

Preservation: Both squamosals are present. The right one is more complete and lacks only a portion of its lateral margin.

Contacts: The squamosal in *Acleistochelys* has the usual bothremydid contacts: quadrate anteriorly, opisthotic medially, and quadratojugal anterodorsolaterally.

Structures: The squamosal in *Acleistochelys* projects posteriorly to a greater extent than in *Azabbaremys* or any other Taphrosphyini except *Labrostochelys*. As in *Azabbaremys*, it lacks the posteroventral vertical flange seen in other Taphrosphyini. It also agrees with *Azabbaremys* and differs from other Taphrosphyini in lacking the lateral tubercle (see Gaffney et al., 2006: Characters 25 and 26). The antrum postoticum is moderate in size in *Acleistochelys*, compared to its absence in *Azabbaremys*, so the squamosal probably contains a cavity for it.

Postorbital

Preservation: Only the anterior part of the right postorbital is present in *Acleistochelys*, and it is broken into two pieces separated by missing bone.

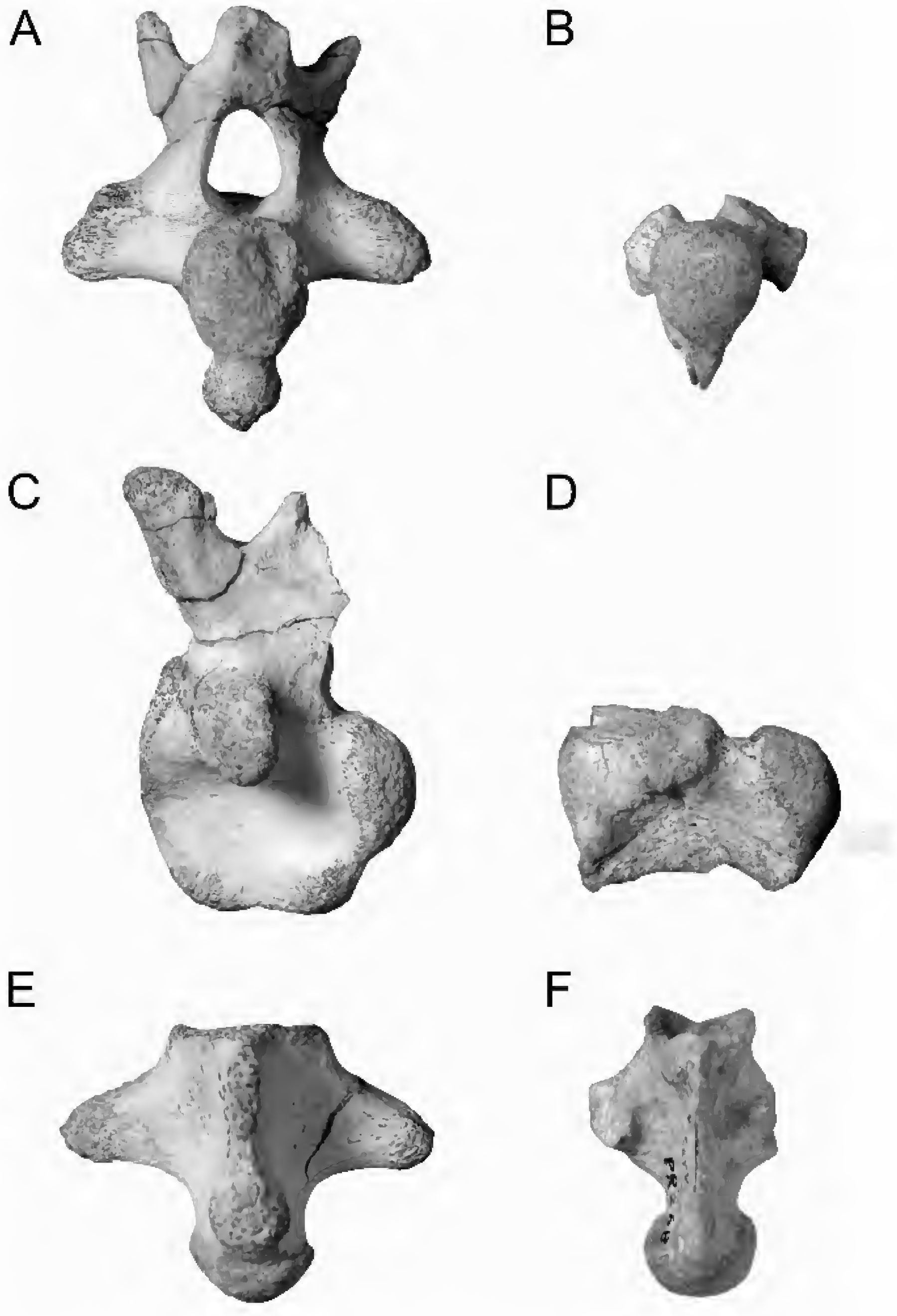

Fig. 8. Cervical vertebrae. A, C, E, *Acleistochelys maliensis* n.gen., n.sp. CNRST SUNY 199; B, D, F, FMNH PR 268 probably *Chedighaii* or *Bothremys*. A, B, posterior views; C, D, left lateral views; E, F, ventral views.

Contacts: As preserved, the postorbital contacts the parietal posteromedially, the frontal anteromedially, and the jugal anteroventrally.

Structures: The medial process of the postorbital that usually forms the dorsolateral part of the septum orbitotemporale, is not formed in *Acleistochelys*, in agreement with all

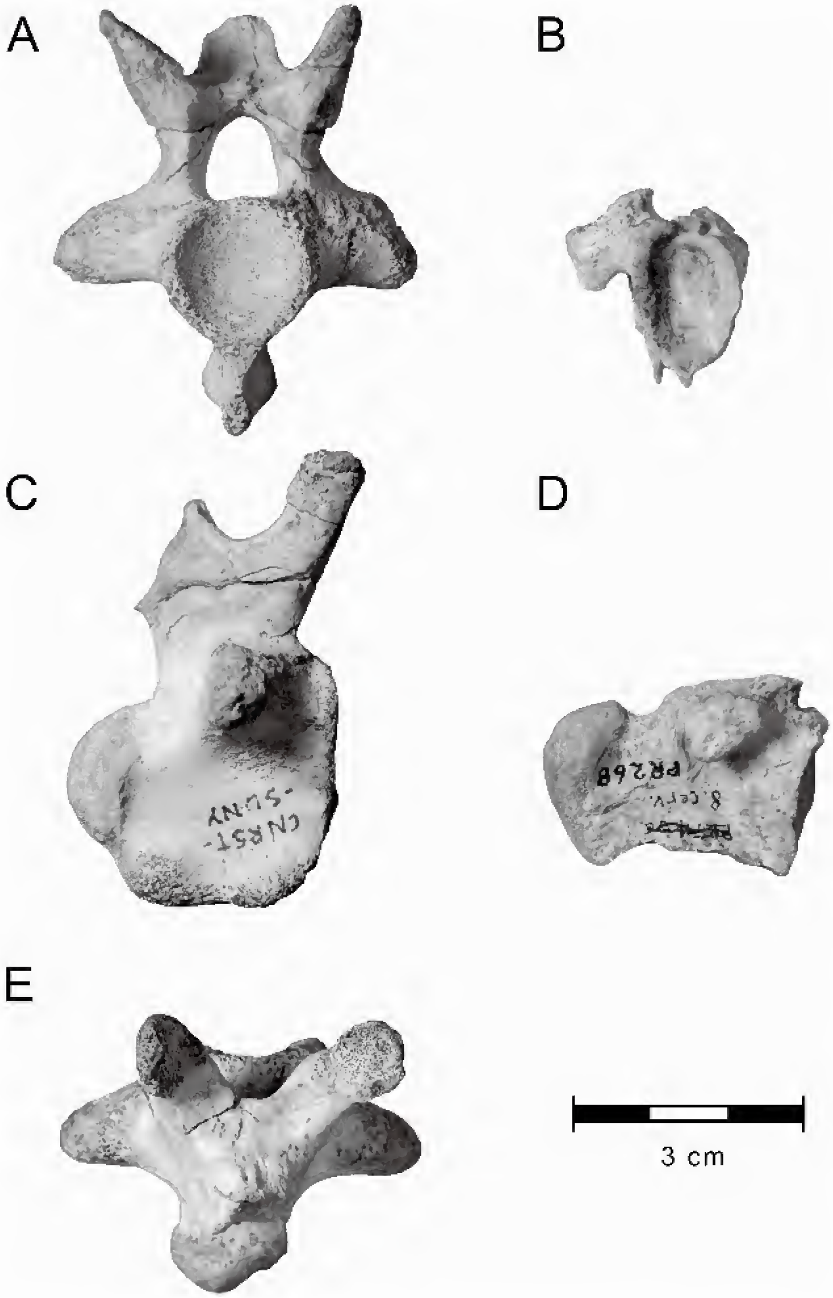

Fig. 9. Cervical vertebrae. A, C, E, *Acleistochelys maliensis* n.gen., n.sp. CNRST SUNY 199; B, D, FMNH PR 268 probably *Chedighaii* or *Bothremys*. A, B, anterior views; C, D, right lateral views; E, dorsal view.

TABLE 2
Cranial Measurements of *Acleistochelys maliensis* (in centimeters)

A. midline length as preserved	18.3
B. maximum width	17.8
C. width between orbits	5.3
D1. width of left orbit	—
D2. width of right orbit	4.5[a]
E. width of external nares	3.6
F. width of internal nares	4.0
G. maximum height at quadrate	11.3
H. width of skull at middle of orbits	9.5
I. length from anterior margin of prefrontals to posterior margin of supraoccipital	14.3[a]
J1. height of left orbit	—
J2. height of right orbit	3.3
K. skull height at occipital condyle	8.5[b]
L. anterior width of triturating surface	2.9
M. posterior width of triturating surface	2.8
N. width of palate across foramina palatinum posterius	6.4
O. length from front of skull to posterior edge of condylus articularis	17.5

[a] damaged.
[b] estimated.

other Taphrosphyini except *Nigeremys* and *Arenila*. There is a low, transverse ridge marking the position of the septum, slightly larger than in *Azabbaremys*.

The postorbital forms the posterodorsal margin of the orbit as in other bothremydids. Its posterior extent is indeterminate.

Premaxilla

Preservation: Both premaxillae are present in CNRST SUNY 199: the right is nearly complete, the left lacks some of the horizontal plate.

Contacts: As in other bothremydids the premaxilla contacts the maxilla posterolaterally and the other premaxilla medially. As in *Labrostochelys*, *Azabbaremys*, *Nigeremys*, and *Arenila*, the premaxilla contacts the vomer posteromedially. In contrast to *Azabbaremys*, the premaxilla in *Acleistochelys* rises to nearly reach the prefrontal along the margin of the aperture narium externa.

Structures on dorsal surface: In contrast to *Azabbaremys*, *Acleistochelys* has a small, median tubercle formed on the midline of the ventral margin of the aperture narium externa.

Structures on ventral surface: The entire triturating surface of *Acleistochelys* is very distinct from that in the other Taphrosphyini, and the premaxillary portion is no exception. The skull in *Acleistochelys* is narrower than in the other members of this group, except *Taphrosphys* and *Labrostochelys*, and the anterior outline of the labial ridge reflects this. The labial ridge formed by the premaxilla is more acute in *Acleistochelys* with respect to the midline than in all other members of the Taphrosphyini. The ridge is thicker than in *Taphrosphys*, but not as thick as in *Azabbaremys*. The ridge has an acute ventral margin as in *Azabbaremys*. The labial ridge in *Acleistochelys* is slightly convex ventrally in anterior view, distinct from the sharper, more defined ventral protuberance seen in *Azabbaremys*.

Acleistochelys has a well-developed accessory ridge on the triturating surface that is morphologically unique among pleurodires. The ridge is expressed anteriorly on the premaxillae and flattens out posteriorly, disappearing about halfway down the maxillary length. The ridge is unusual in being broad anteroposteriorly on the premaxilla, which is defined anteriorly by a narrow trough and posteriorly by a median concavity on the posterior half of the premaxilla. There is no midline concavity as in *Azabbaremys* and other members of the Taphrosphyini. The premaxilla of *Acleistochelys* is much longer than that in *Azabbaremys*. A long premaxilla also occurs in *Nigeremys* and *Arenila*, but the morphology of the triturating surface is much simpler in those species, lacking an accessory ridge. The strong corrugations unique to *Azabbaremys* are completely absent in *Acleistochelys*.

Maxilla

Preservation: Both maxillae are present. The left one lacks the anterior part of the horizontal plate, the right one lacks the posteroventral end of the vertical plate. Together all of the maxilla morphology is available.

Contacts of vertical plate: As in other Taphrosphyini, the maxilla of *Acleistochelys* contacts the premaxilla anteromedially, the prefrontal anterodorsally, the jugal posterodorsally, and the quadrate posteroventrally.

Structures of vertical plate: The maxilla barely enters the margin of the apertura narium externa in contrast to the wider condition in other Taphrosphyini. The maxilla forms the anteroventral margin of the orbit, but it is less extensive than in *Azabbaremys*. The ventral margin of the maxilla trends slightly ventrally to meet the quadrate; there is no indication of a cheek emargination.

Contacts of horizontal plate: On the dorsal surface the maxilla contacts the jugal posteriorly and the palatine posteromedially. On the ventral surface the maxilla contacts the premaxilla anteromedially in a long suture, but does not reach the vomer.

Structures of horizontal plate: The labial ridge of the maxilla in *Acleistochelys* is thinner than that ridge in *Azabbaremys* and *Nigeremys*, but much thicker than in *Ummulisani* and *Labrostochelys*. The accessory ridge developed on the premaxilla extends onto the anterior part of the maxilla, but flattens posteriorly and disappears well anterior to the posterior end of the triturating surface. The triturating surface is parallel-sided with no distinct lingual ridge marking its medial limit.

The triturating surface has a shallow but distinct pit at its posterior-most margin, formed by the maxilla anteriorly, the palatine medially, and the jugal posteriorly (see Jugal). The shallow trough marking the medial edge of the labial ridge, much deeper anteriorly, leads into the pit.

The maxilla forms the anterior part of the floor of the fossa orbitalis. It forms part of the distinct ridge that forms the orbital margin. The maxilla forms most of a dorsally opening concavity or fossa in the anterior part of the orbital floor. This is probably homologous to the ventral pocket seen in *Ummulisani* (Gaffney et al., 2006: fig. 211B, "fossa orbitalis ventral pocket"), but the fossa in *Acleistochelys* is much smaller than the one in *Ummulisani*. A ventral concavity also occurs in other members of the Taphrosphyini, but the morphology is variable. *Azabbaremys* also has a concavity formed by the maxilla, but it is farther posterior than in *Acleistochelys*.

Vomer

The single vomer is present in CNRST SUNY 199. It seems to be complete, but is bent slightly to the right. Its completeness is an issue because as preserved it has the unusual morphology of being wide anteriorly where it has a solid contact with the premaxillae, and narrows posteriorly ending at a point before reaching the palatines in strong contrast to other turtles that have a solid palatine contact. The interesting feature of this morphology is that it also occurs in *Azabbaremys* (Gaffney et al., 2006: fig. 216), but not in other members of the Taphrosphyini. It is one of the two characters holding *Acleistochelys* and *Azabbaremys* together, the other being an absence of the vomer-maxilla contact (Gaffney et al., 2006: characters 44, 47). In the single specimens available of *Azabbaremys* and *Acleistochelys* there is no sign of a broken edge along the length of the vomer, and the vomers in each seem to be well preserved. However, *Acleistochelys*, in contrast to *Azabbaremys*, is missing the anterior margin of the palatines, so no supporting examination of that morphology is possible.

Palatine

Preservation: Both palatines are present and are complete except for their anterior margins, which are broken and lacking a finished edge. Their dorsal surfaces are visible but broken medially with some areas unclear.

Contacts: The palatine contacts the maxilla anterolaterally, the other palatine medially, the pterygoid posteriorly and laterally, and the jugal anterolaterally, all of which occur in other members of the Taphrosphyini. *Acleistochelys* is unique, however, in having a strong posteromedial contact with the basisphenoid, correlated with the very large size of the palatines and the relatively small size of the pterygoids. The related separation of the pterygoids on the midline is also unique to *Acleistochelys* among the members of the Taphrosphyini. It is possible that the palatines reach the basisphenoid in the poorly preserved

Nigeremys, but the known sutures are not similar to those in *Acleistochelys*.

On the dorsal surface the palatine in *Acleistochelys* contacts the parietal just lateral to the sulcus palatinopterygoideus.

Structures on dorsal surface: The dorsal surface of the palatine in *Acleistochelys* forms the medial part of the floor for the fossa orbitalis and the medial part of the low, transverse ridge marking the remnant of the septum orbitotemporale (see also Jugal). In all of the members of the Taphrosphyini, except *Nigeremys* and *Arenila*, the septum orbitotemporale is partially or completely open. In the case of *Acleistochelys* and *Phosphatochelys* more of the septum is present than in *Taphrosphys*, *Azabbaremys*, and *Rhothonemys*. In *Acleistochelys* and *Phosphatochelys* there is a ventral process of the parietal (see Parietal) that meets at least the palatine and forms a partial lateral limit to the sulcus palatinopterygoideus (Gaffney et al., 2006: Introduction to Pleurodire Skull Morphology). In *Acleistochelys* the palatine contacts the parietal dorsally, the jugal anteroventrally and the pterygoid posteroventrally. In *Phosphatochelys* the palatine contacts the parietal dorsally and the pterygoid posteriorly. In *Azabbaremys* the palatine has no dorsal contacts and bears only a low ridge in the position of the septum orbitotemporale. The other members of the Taphrosphyini are either too incomplete or covered with matrix in the area, preventing palatine comprehension.

Structures on ventral surface: The palatine in *Acleistochelys* forms the high choanal arch, similar to that in *Azabbaremys*. Although the arched palate is actually higher in *Azabbaremys* than in *Acleistochelys*, in *Acleistochelys* the palatine curves ventrally along its lateral edge to form a parasagittal, vertical wall that is a posterior continuation of the apertura narium interna margin, a morphology very different from *Azabbaremys* and the other members of the Taphrosphyini.

Quadrate

Preservation: Both quadrates are present but incomplete in CNRST SUNY 199. The processus articularis, medial process, and central area of the cavum tympani are present on both sides, but the anterior margin, anterior part of the cavum tympani and some of the dorsal margin are missing on both sides.

Contacts on lateral surface: The anteroventral contact with the maxilla is present on the left side, and there are small fragments of the quadratojugal on both sides, but the contacts of the jugal and postorbital with relation to the quadrate are indeterminate. The squamosal is present on both sides in its unalterable position.

Structures on lateral surface: Little indication of the temporal extent remains on the quadrate, but the left side seems to show a natural edge similar to that in *Azabbaremys* indicating emargination of at least the extent seen in that form.

The cavum tympani is incomplete, but what is present shows the incisura columellae auris as a fully enclosed canal and the sulcus eustachii as a narrow groove posteroventral to the incisura columellae auris, as in *Azabbaremys* and other members of the Taphrosphyini. The area where the fossa precolumellaris should be absent is not preserved. The ventral shelf seen in many other members of the Bothremydidae is present. The antrum postoticum seems to be present on the left side and is moderate in size, in the scheme of Gaffney et al. (2006). This would agree with *Nigeremys*, *Arenila*, and *Rhothonemys*, in contrast to *Azabbaremys*, which has a completely filled incisura columellae auris.

Contacts on dorsal and anterior surface: The quadrate contacts the prootic anteromedially, the opisthotic posteromedially and the squamosal posterolaterally as in other members of the Taphrosphyini. However, in contrast to all other members of this group (indeterminate in *Nigeremys* and *Arenila*) there is a supraoccipital-quadrate contact visible on both sides in *Acleistochelys*. This contact is a Bothremydidae synapomorphy, reversed in the Taphrosphyini, so its presence in *Acleistochelys* is either a retained primitive condition for Bothremydidae or a reversal.

Structures on dorsal and anterior surface: The foramen stapedio-temporale in *Acleistochelys* opens anteriorly and lies close to the foramen nervi trigemini (see Gaffney et al., 2006, for distribution of these characters).

Contacts on ventral surface: As in other members of the Taphrosphyini, the quadrate in *Acleistochelys* contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially. The extent of contact with these elements varies a great deal within this group (Gaffney et al., 2006: fig. 11). In *Acleistochelys* these contacts are roughly similar to those seen in *Labrostochelys*, in contrast to the much narrower basisphenoid contact of *Azabbaremys*.

Structures on ventral surface: The fossa pterygoidea is absent in all members of the Taphrosphyini except *Nigeremys*, *Arenila*, and *Acleistochelys*. In *Acleistochelys* the fossa is deep, with a strong anterolateral wall of quadrate and the foramen posterius canalis carotici interni in the anterior part of its roof. In the cladogram of Gaffney et al. (2006: fig. 288) the deep and narrow fossa pterygoidea evolves three times independently: in *Acleistochelys*, in *Nigeremys* + *Arenila*, and in *Foxemys* + *Polysternon*. *Azabbaremys* and *Acleistochelys* are only weakly resolved. Moving *Acleistochelys* to the group *Nigeremys* + *Arenila* results in a cladogram only one step longer than the shortest.

The foramen posterius canalis carotici interni in *Acleistochelys* is formed by the pterygoid anteriorly, the quadrate posterolaterally, and the basisphenoid posteromedially. Within the members of the Taphrosphyini, only *Taphrosphys* agrees with *Acleistochelys* in having these three bones form the foramen. However, the formation of the fossa pterygoidea is apparently associated with the more dorsal position of the foramen posterius canalis carotici interni (Gaffney et al., 2006). In *Azabbaremys* the foramen is formed by the pterygoid and quadrate. The excavation of the fossa pterygoidea could result in the exposure of the more dorsal portion of the basisphenoid, so the canalis carotici interni would appear to have moved dorsally. Despite the attraction of this elegant hypothesis, the presence of the same condition in *Taphrosphys*, which completely lacks a fossa pterygoidea, makes it dubious.

The condylus mandibularis in *Acleistochelys* is slightly anterior to the position of the condylus occipitalis. This is coded as "near or on plane of basioccipital-basisphenoid suture" in Gaffney et al. (2006: Character 60). The condylus mandibularis in *Acleistochelys* is just posterior to the suture. In *Azabbaremys* the condylus mandibularis is slightly more posterior but still similar in position. This is in contrast to the more posterior position of the condylus mandibularis in *Nigeremys* + *Arenila*.

Contacts on posterior surface: As in the other members of the Taphrosphyini, the quadrate in *Acleistochelys* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the exoccipital medially.

Structures on posterior surface: The fenestra postotica in *Acleistochelys* is an oval opening completely enclosed by the quadrate ventrally and the opisthotic dorsally. There is no subdivision of the fenestra postotica.

Pterygoid

Preservation: Both pterygoids are present, the left one is nearly complete lacking some of the edge of the processus trochlearis pterygoidei and some of the crista pterygoidea. The right pterygoid lacks the lateral part of the processus trochlearis pterygoidei.

Contacts on ventral surface: The pterygoid in *Acleistochelys* is unusually shaped. The common transverse contact with the palatine seen in most turtles is sharply angled anterolateral to posteromedial to such an extent that the nearly universal medial contact of the pterygoids is lost in *Acleistochelys*. Some bothremydids do have a very short pterygoid contact (see Gaffney et al., 2006), but they do not lose the contact. *Acleistochelys* has a long anterolateral process of the pterygoid extending along the palatine to reach the jugal near the foramen palatinum posterius, as in nearly all turtles. The pterygoid in *Acleistochelys* contacts the basisphenoid medially and the quadrate posterolaterally.

Structures on ventral surface: The processus trochlearis pterygoidei is present on both sides of CNRST SUNY 199. The right one is broken, but most of the process seems to be present on the left. As in other members of the Taphrosphyini, the processus trochlearis pterygoidei is relatively small compared with other bothremydids and podocnemidids. Although some of the thin edge and much

of the flange is broken away, the preserved size seems to be close to its original size because the preserved bone is very thin and tapered along the broken margin.

The fossa pterygoidea (see Quadrate) is deep and narrow, as in *Nigeremys* + *Arenila*. It is formed by the pterygoid anteriorly, the quadrate posterolaterally, and the basisphenoid posteromedially. The foramen posterius canalis carotici interni (see Quadrate) lies in the anterior part of the roof of the fossa pterygoidea and is formed by the pterygoid, quadrate, and basisphenoid. On both sides there is a small foramen, anterior to the foramen posterius canalis carotici interni but within the fossa pterygoidea, that leads into a canal running anteriorly in the pterygoid. This foramen appears to be the foramen nervi vidiani, which occurs in this position in some other bothremydids (Gaffney et al., 2006: figs. 276, 277).

The foramen palatinum posterius is formed anteromedially by the palatine and posterolaterally by the pterygoid. In most bothremydids this suture is transverse, but in *Acleistochelys* it is sharply oriented posteromedially and the foramen palatinum posterius has retained its position in the suture but not the palate in general.

Contacts on dorsal surface: The pterygoid in *Acleistochelys* contacts the palatine anterodorsally and the jugal anteriorly at the base of the processus trochlearis pterygoidei, but due to the near absence of the septum orbitotemporale there is no postorbital contact. The crista pterygoidea contacts the parietal dorsally in its anterior part, then the quadrate posterior to the foramen nervi trigemini.

Structures on dorsal surface: The dorsal surface of the pterygoid in *Acleistochelys* has the relatively narrow crista pterygoidea, similar to that in *Azabbaremys*. The sulcus palatinopterygoideus is relatively open laterally in *Acleistochelys*, but its floor is formed by the palatine anteriorly and the pterygoid posteriorly. The pterygoid also forms a low wall along the lateral margin of the sulcus, from the processus trochlearis pterygoidei to the narrow dorsal process marking the anterior remnant of the sulcus palatinopterygoideus.

Supraoccipital

Preservation: The ventral body of the supraoccipital in CNRST SUNY 199 is largely complete, although some is missing in cracks on the left side, and there is a slight amount of lateral distortion. The crista supraoccipitalis, however, is broken away and the dorsal part of the supraoccipital, although present, is displaced.

Contacts: The supraoccipital of *Acleistochelys* has the usual contacts found in members of the Taphrosphyini: parietals dorsally and anteriorly, prootic anterolaterally, opisthotic posterolaterally, and exoccipitals posteroventrally. In addition, and unique among this group, there is a quadrate contact laterally (see Quadrate). This is clear and visible on both sides, formed in the usual bothremydid manner by a lateral lappet of supraoccipital.

Structures: The crista supraoccipitalis is broken off close to its base, but the broken edge is relatively high and thick, more so than in *Azabbaremys*. The foramen magnum is higher than wide and oval, as in *Azabbaremys*.

Exoccipital

Preservation: Both exoccipitals are present and nearly complete in CNRST SUNY 199, with a slight amount of dorsoventral distortion.

Contacts: As in other bothremydids the exoccipital of *Acleistochelys* contacts the supraoccipital dorsally, the opisthotic dorsolaterally, the quadrate ventrolaterally and the basioccipital ventrally.

Structures: The condylus occipitalis in *Acleistochelys* is formed mostly by the two exoccipitals with the basioccipital entering the condylus articularis surface slightly. This is unusual for most advanced bothremydids, which have the basioccipital excluded from the articular surface and restricted to the neck of the condylus occipitalis.

The foramen nervi hypoglossi is a single, large opening in *Acleistochelys*, in contrast to the usual two or more smaller openings seen in other bothremydids. The foramen nervi hypoglossi is just dorsolateral to the neck of the condylus occipitalis,

opening ventrolaterally. In *Azabbaremys* the foramen is smaller, paired, and placed more dorsally.

The foramen jugulare posterius in *Acleistochelys* is closed by the dorsal and ventral plates of the exoccipital with a thin process of quadrate between them, as in *Azabbaremys*.

Basioccipital

Preservation: The basioccipital in CNRST SUNY 199 is nearly complete but visible only ventrally.

Contacts: As in other bothremydids, the basioccipital of *Acleistochelys* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipital posterodorsally.

Structures: The basioccipital slightly enters the articular surface of the condylus occipitalis (see Exoccipital). There is a relatively deep, median concavity, facing posteroventrally, formed by basioccipital and basisphenoid, not seen in *Azabbaremys* but present in the *Nigeremys* + *Arenila* group. The basioccipital of *Acleistochelys* is relatively short as in *Azabbaremys*.

Prootic

Preservation: Both prootics are present and relatively well preserved, although the right one is a little chewed on ventrally.

Contacts: As in the other members of the Taphrosphyini, the prootic of *Acleistochelys* contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally. Uniquely among this group, there is no opisthotic contact due to the supraoccipital lappet contacting the quadrate (see Quadrate). It is extremely likely that an opisthotic-prootic contact underlies the supraoccipital lappet as in the other bothremydids.

Structures: The prootic of *Acleistochelys* has an almost cryptodiran anterior overhang, above the foramen nervi trigemini and foramen stapedio-temporale. Neither foramen is visible in dorsal view and both are close together (Gaffney et al., 2006). The foramen nervi trigemini is formed by the prootic posterodorsally, the parietal anterodorsally, the pterygoid anteroventrally, and a small sliver of quadrate seems to enter it posteroventrally. The quadrate rarely enters the foramen nervi trigemini, but, as in *Phosphatochelys* and *Taphrosphys* (at least), the sulcus cavernosus is exposed in the enlarged foramen and the quadrate forms part of the sulcus cavernosus.

The foramen stapedio-temporale is poorly preserved on the right side, but is clearly visible on the left. It lies in the prootic-quadrate suture, but is more dorsal than that foramen in *Azabbaremys*. The foramen has an irregular shape in CNRST SUNY 199, possibly due to erosion of the thin bone along its lateral margins. The foramen is at the lateral end of a groove that extends ventromedially into the sulcus cavernosus and foramen nervi trigemini, as seen in *Azabbaremys* and some other bothremydids that have this area well preserved. Despite the deep fossa pterygoidea on the ventral surface of the skull, there is no exposure of the prootic.

Opisthotic

Preservation: Both opisthotics are present; the left one is missing its dorsomedial part.

Contacts: As in the other bothremydids, the opisthotic of *Acleistochelys* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. There is no external prootic contact due to the supraoccipital-quadrate contact.

Structures: The fenestra postotica is formed by the opisthotic dorsally and by the quadrate ventrally. It is completely enclosed as in other members of the group *Taphrosphys* and its close relatives. The fenestra is oval, with a strong horizontal shelf overhanging it dorsally, and similar in shape to that seen in *Azabbaremys*.

Basisphenoid

Preservation: The basisphenoid in CNRST SUNY 199 is complete but not visible dorsally.

Contacts: The basisphenoid of *Acleistochelys* is similar in size and shape to that in *Azabbaremys* and *Nigeremys*, but has a broad

anterior contact with the palatines, uniquely among bothremydids. Anterolaterally the basisphenoid contacts the pterygoids, posteriorly the basioccipital, and posterolaterally the quadrate.

Structures: The basisphenoid in *Acleistochelys* is triangular in shape with a lateral process curving anterolaterally into the fossa pterygoidea. In the fossa pterygoidea the basisphenoid forms part of the foramen posterius canalis caroticus interni, along with the pterygoid and quadrate (see Pterygoid). The basisphenoid forms the anterior margin of a midline concavity (see Basioccipital).

POSTCRANIAL MORPHOLOGY

There are a large number of shell fragments associated with the type skull, as well as some postcranial bones. Among the more useful shell elements are a first neural, a fourth neural, part of the nuchal, and an anterior peripheral fragment. The carapace elements are all relatively thick; the first neural averages 2.1 centimeters for an element 10.9 centimeters in length.

The first neural bone in *Acleistochelys* is four-sided with the first vertebral-second vertebral sulcus running transversely across it as in other Pelomedusoides. The orientation of the first neural is unclear, but the most likely anterior direction has been chosen by comparison with *Taphrosphys*. It seems to be slightly thinner from side to side in this direction, as in *Taphrosphys*.

The fourth neural is identified as such because it lacks an intervertebral sulcus, making it either number two or number four, and its anterior sutural surface does not mate with neural one so it must be neural four. On the ventral surface of the neurals is the longitudinal ridge that is fused to the neural spine of the thoracic centra. Some fragments of thoracic centra are present but do not articulate with the neurals.

The nuchal bone of CNRST SUNY 199 is represented by the anterior margin from the midline to the left contact with the first peripheral. The midline sulcus is present and shows that a cervical scale is absent, as in all other Pelomedusoides. As with the neurals, the bone is very thick, but restoring the width of the neural at 27 cms results in a very large shell when extrapolated, so the thickness may be just a function of size. The nuchal in *Acleistochelys* has a transverse anterior margin, as in *Taphrosphys*, not embayed as in *Chedighaii*. The anterior edge of the nuchal is rounded and relatively obtuse rather than thin and acute as in *Taphrosphys*. Laterally the edge becomes even thicker in *Acleistochelys*, also in contrast to *Taphrosphys* in which it is acute and thin for its entire width.

One of the many carapace fragments may be the posterior position of peripheral two. It has the posterior sutural surface preserved, but lacks its anterior half and medial margin. The sulci for marginal two-marginal three and vertebral one-marginal three are present and shows that the marginals are distal to the peripheral-costal suture, as in other bothremydids. As with the nuchal, the free margin of the peripheral is thick and obtuse, with a rounded edge.

A single cervical, lacking its neural spine, is present in CNRST SUNY 199. It is procoelus, as in cervicals 2-8 of all other Pelomedusoides (Williams, 1950). Unfortunately, cervical vertebrae of bothremydids are very poorly known, and only fragments exist of *Taphrosphys, Bothremys*, and *Chedighaii*. The more complete ones are a centrum lacking the entire neural arch, FMNH PR 268, either *Bothremys* or *Chedighaii*; and a nearly complete cervical, FMNH 247, *Bothremys*. There are some neural spines known for *Taphrosphys sulcatus*, but as this area is broken off in CNRST SUNY 199, they are not relevant. The *Acleistochelys* cervical is not determinable as to position; it is probably more posterior in the series based on general size and shape comparison with *Pelusios* and *Pelomedusa*. The *Acleistochelys* and Bothremydini centra differ significantly from pelomedusids in being much higher and shorter and with a deep ventral process. The *Acleistochelys* cervical is very similar to the Bothremydini cervicals differing from FMNH PR 247 in being longer with a narrower ventral process. The *Acleistochelys* cervical is nearly identical to FMNH PR 268. The differences with PR 247 could be the result of relative position in the column. The bothremydid cervicals have prominent transverse processes, also found in

recent pleurodires. The central articulations in the bothremydids are nearly circular; the ones in pelomedusids vary from circular to wider than high. The base of the neural arch in the three bothremydid cervicals is much narrower than in pelomedusids. So the *Acleistochelys* cervical agrees with the Bothremydini cervicals, but the systematic significance of this is unknown at present.

The *Acleistochelys* carapace elements show an irregular surface texture that is similar to but not as well defined as that seen in *Taphrosphys sulcatus*. The texture consists of anastomosing furrows forming raised humps.

SUMMARY

Acleistochelys maliensis is a new bothremydid side-necked turtle from the Paleocene Teberemt Formation of Mali. It is based on a single individual with a well-preserved skull and a few postcranial fragments. Characters of the skull indicate that it is most closely related to *Azabbaremys moragjonesi* also from the Paleocene Teberemt Formation of Mali. Although the phylogenetic analysis (Gaffney et al. 2006) places these two as sister taxa, based on the narrow, posteriorly unattached vomer, the skulls differ in many morphologic features. Compared with *Azabbaremys, Acleistochelys* has a narrower skull, a narrower triturating surface with a small pit and no corrugations and an accessory ridge, a jugal exposed on the triturating surface, a wide palatine-basisphenoid contact separating the pterygoids, a supraoccipital-quadrate contact, a fossa pterygoidea, and a foramen posterius canalis carotici interni formed by the pterygoid, basisphenoid, and quadrate.

The narrow skull, narrow and smooth triturating surfaces, and fossa pterygoidea present in *Acleistochelys* also occur in *Arenila*, another Taphrosphyini from the Maastrichtian of Egypt. In the cladogram of Gaffney et al. (2006: fig. 288) the deep and narrow fossa pterygoidea evolves three times independently: in *Acleistochelys*, in *Nigeremys + Arenila,* and in *Foxemys + Polysternon*. *Azabbaremys* and *Acleistochelys* are only weakly resolved. Moving *Acleistochelys* to the group *Nigeremys + Arenila* results in a cladogram only one step longer than the shortest. So the possibility of a close relationship of *Acleistochelys* with *Arenila* and its close relative, *Nigeremys,* should be kept in mind.

The presence in the near-shore marine sediments of Mali of two large species of closely related bothremydid pleurodires is not unusual. The near-shore marine phosphates of the North African Paleogene have yielded over a dozen taxa of pleurodires in recent years (Gaffney et al. 2006), and it was clearly an area of bothremydid diversification in the Paleogene.

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